



Every scar has a story: age and sex-specific conflict rates in wild bottlenose dolphins

Harry H. Lee¹ · Megan M. Wallen¹ · Ewa Krzyszczyk¹ · Janet Mann^{1,2}

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Abstract

Social living brings competition over mates, relationships, and resources, which can translate to direct conflict. In dolphins, tooth rakes received from conspecifics are highly visible and reliable indicators of conflict. New rakes indicate recent conflicts while healed rakes suggest older instances of conflict. Here, we investigate the healing time of conspecific tooth rakes in wild bottlenose dolphins, create a demographic profile of injury risk in the population, and consider the implications for age- and sex-specific aggression. Using photographic and scarring data from the Shark Bay Dolphin Research Project spanning 31 years ($N = 269$ tooth rakes), healing time was analyzed using a subset of sequential photographs of the same body part over 1–12 years ($N = 70$ tooth rakes). Ninety percent of tooth rakes in males and 95% of tooth rakes in females were no longer visible within 400 days, with males taking longer to heal than females. Using the full sample, we examined age and sex-effects on the prevalence of new tooth rakes. A negative quadratic model best fitted tooth rake prevalence patterns from ages 0 to 13 and a positive linear regression best fitted tooth rake prevalence patterns from ages 13 to 30. Both analyses revealed significant age and sex effects, where males had more tooth rakes than females. Age differences in tooth rake prevalence may be attributed to life history events such as sexual maturity onset, male-male competition and alliance formation, and sexual coercion. These results contribute to our understanding of the relationship between social conflict and life history strategies in long-lived mammals.

Significance statement

In wild dolphins, tooth rake scars indicate conspecific conflict, and the timing of such conflict clarifies the challenges faced during each life history stage. Based on > 30 years of longitudinal data, we created a demographic profile of new tooth rakes to identify patterns of age- and sex-specific received aggression. Males had more tooth rakes than females, but females healed faster than males. Juveniles had the greatest tooth rake prevalence compared to calves and adults, suggesting greater exposure to some level of conflict. Differences in patterns of tooth rake prevalence and aggression have implications regarding the costs of sexual maturity and reproduction in dolphins. To our knowledge, no study has examined the rate of received aggression across the lifespan. Our methods can be applied to other studies of wild marine mammals, where agonistic encounters are difficult to observe, but wounds are apparent.

Keywords Aggression · Healing · Intraspecific conflict · Lifespan · Tooth rakes · *Tursiops*

Introduction

Social living results in competition over resources, mates, and relationships (Alexander 1974; Parrish and Edelman-Keshet 1999; Huchard and Cowlishaw 2011), which often translates to instances of overt conflict. The degrees of conflict vary according to resource availability and the social context (van Schaik 1999; Connor et al. 2000; Shen et al. 2014). In response, social living species adjust aspects of their group structure, such as size and physical cohesiveness (van Schaik 1999; Shen et al. 2014). Life history strategies can also

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✉ Harry H. Lee

¹ Department of Biology, Georgetown University, Washington, DC 20057, USA

² Department of Psychology, Georgetown University, Washington, DC 20057 USA

impact grouping and competition. For example, females with dependent offspring group to reduce predation risk (Sterck et al. 1997; Fleagle 2013). Males often leave their natal group when reaching sexual maturity and are vulnerable on their own until they can join a new social group (Dobson 1982; Glander 1992; Sprague 1992; Breuer et al. 2009). Here, we examine received conflict across the lifespan among wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), a species known for high intrasexual and intersexual conflict (Connor et al. 1996; Scott et al. 2005; Cords and Mann 2014; Wallen et al. 2016).

Socio-ecological theory highlights the types of competition that occur among mammals and the effects they have on social relationships (van Schaik 1999; Janson 2000; Dammhahn and Kappeler 2009). Among social living mammals, group size is constrained by indirect or scramble competition for food (Janson 2000; Harris et al. 2010). Similarly, aggressive or contest competition affects social cohesion and, in some circumstances, can favor alliance formation (Janson 2000). In contest competition, individuals increase fitness by acquiring more resources, such as mates (males: Smuts and Smuts 1993; MacCormick et al. 2012; Orbach et al. 2014) or food (females: Clark 1978; Isbell 1991; Schülke 2003; Clutton-Brock 2007; Rosvall 2011), than their competitors (Van den Berg et al. 2006).

To reduce direct competition, some mammalian taxa such as elephants, bats, primates, and bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*), have dynamic patterns of fission-fusion grouping (van Schaik 1999; Archie et al. 2006; Popa-Lisseanu et al. 2008; Galezo et al. 2018). In fission-fusion societies, individuals have core networks or communities, but move between smaller or larger groups that regularly change in composition. Factors such as kinship (e.g., African savannah elephants, *Loxodonta africana*, Archie et al. 2006), social bonds (e.g., Bechstein's bats, *Myotis bechsteinii*, Kerth et al. 2006), and activity state (bottlenose dolphins, Gero et al. 2005; Galezo et al. 2018) drive these dynamics.

Among Indo-Pacific bottlenose dolphins of Shark Bay, Australia, fission-fusion dynamics are high, with group composition changing on average six times an hour (Galezo et al. 2018). Dolphins forage alone and group to rest or socialize (Galezo et al. 2018). Adult males form alliances with other males in response to intra- and inter-sexual competition. Male dolphins of the same alliance cooperate to increase mating success by collectively consorting with females and limiting the target female's access to other males (Connor and Krützen 2015). Alliances can range in size from two to 14 dolphins and are characterized by cooperation within an alliance when in conflict with females and other males (Connor and Krützen 2015). Among female Indo-Pacific bottlenose dolphins, acts of aggression are exceedingly rare (Mann and Smuts 1999; Scott et al. 2005). As dolphins catch their own fish, there is no

contest competition over prey resources in the Shark Bay dolphin population (Mann and Sargeant 2003; Mann et al. 2007). The sole exception is at a provisioning site in Shark Bay, Monkey Mia, where up to five adult females receive fish handouts from tourists. Occasional aggression is observed among females over this concentrated and defensible resource (Foroughirad and Mann 2013).

Although observations of contest competition are rare; products of conspecific aggression, including physical wounds such as tooth rakes, serve as evidence of aggressive behavior, thus providing insight regarding the nature of intra-specific competition. For example, a recent study used skin lesions, resulting from received bites, to measure contest cost and intensity in pigs (Camerlink et al. 2017). Physical wounds such as gashes, cuts, or punctures of the skin have been used to assess aggression in primates as well (Olive baboon, *Papio anubis*, MacCormick et al. 2012; Chimpanzee, *Pan troglodytes*, Muller and Mitani 2005).

The developmental timing of conspecific conflicts is critical for understanding the costs and benefits of group living, which vary by age, sex, and reproductive and social status. For example, in a study of olive baboons, both sexes had the most wounds at ages when competition over dominance rank was the most intense. Immigrant males attempting to join a new group acquired more wounds than resident males. Females had fewer wounds, largely explained by the fact that female ranks are determined by maternal social inheritance and defense and less by escalated fights (MacCormick et al. 2012).

Age and sex are key demographic factors that correlate with social conflict and population dynamics (Martin 1995; Gaillard et al. 2000; Dreiss et al. 2010). Life history events, such as weaning, maturation, and reproductive status, can perpetuate conflict. For instance, among ring-tailed coatis (*Nasua nasua*), juveniles directed considerable aggression towards older and larger individuals (Hirsch 2007). Hirsch (2007) suggests that this may be an example of "tolerated aggression" and is a way for physically inferior juveniles to increase their access to food during a critical growth period. In contrast, the rate of aggression decreased over ontogeny in spotted hyenas (*Crocuta crocuta*), largely because dominance rank is established early in this species (Turner et al. 2018). Juvenile bison bulls (*Bison bison*) tend to be aggressive with their similar sized male partners, as possible training for future encounters (Rothstein and Griswold 1991). Male prairie voles decrease prosocial behavior and increase aggression with age, when it is likely to enhance fitness (Kelly et al. 2018).

Shark Bay Indo-Pacific bottlenose dolphins are often alone in the juvenile period (Krzyszczuk et al. 2017) and no longer under maternal protection; this is especially the case for males who associate less with their mothers post-weaning than females (Tsai and Mann 2013). As such, juvenile males might be particularly vulnerable to aggression from older males. This assertion is supported by the fact that, within the Shark

Bay dolphin population, calf social network centrality predicts juvenile stage survival for males (Stanton and Mann 2012). Previous findings have also shown that juvenile males have higher mortality than juvenile females (Stanton and Mann 2012).

Specific challenges of adulthood may precipitate conspecific conflict, particularly male-male, but also male-female. Studies on wild baboons have found that cycling females exhibit higher incidence of wounds than their non-cycling counterparts, suggesting a relationship between reproductive state and conspecific conflicts (MacCormick et al. 2012; Archie et al. 2014). This pattern holds true for dolphins, as cycling females have a higher incidence of new tooth rakes than non-cycling females (Scott et al. 2005). Sex differences in aggression and sexual competition (male-male or male-female) have been inferred by scarring in a variety of cetacean species (McCann 1974; Best 1979; Silverman and Dunbar 1980; Payne and Dorsey 1983; Heyning 1984; Gerson and Hickie 1985; Chu and Nieukirk 1988; Tolley et al. 1995; Scott et al. 2005; Martin and da Silva 2006; Rowe and Dawson 2009; Coomber et al. 2016). In fact, tooth rake scarring can be a reliable indicator of sex in some species (e.g., Cuvier's beaked whales *Ziphius cavirostris*, Coomber et al. 2016; Indo-Pacific humpback dolphins *Sousa chinensis*, Wright et al. 2017). New tooth rakes indicate recent conflict, but the older the tooth rake, the more difficult it is to accurately determine when the conflict occurred. Lockyer and Morris (1990) found that healing rate is dependent on the severity of the injury; superficial scratches and wounds can take anywhere from a few months to 20 months to become completely indiscernible. As such, healing status can be used as an indicator of the timing of aggression. These findings underscore the links between scarring and patterns of conspecific aggression within and between the sexes.

Although some studies have examined sex differences in conspecific aggression in cetaceans, no study has investigated how these patterns might change over a lifetime or during key life history transitions. To do so, one needs detailed life history data and a large sample size. Such information could shed light on critical life stages and when animals are most vulnerable to conspecific attacks (e.g., weaning, alliance formation, reproduction). Our objectives were to determine (1) the healing time of conspecific tooth rakes in wild Indo-Pacific bottlenose dolphins and (2) the demographic (age and sex) profiles of conflict rates in the population.

We hypothesized that age would impact conflict rate, as indicated by the prevalence of new tooth rakes, particularly among males. Male juveniles may be more susceptible to attacks than male calves, and likely acquire tooth rakes during play, intrasexual competition, and sexual practice (Scott et al. 2005). Sexual coercion of adult females by males is evident from scarring and behavioral observations (Connor et al. 2000; Scott et al. 2005; Wallen et al. 2016). However, adult

females might not all be equally vulnerable. Watson-Capps (2005) found that young adult females receive more aggression from adult males than older females. The reasons behind this may be multifold. Sexual coercion may be higher towards younger females because they have higher calving success than older females (Karniski et al. 2018). Alternatively, or in addition, older females may have learned how to respond to, counter, or avoid sexual coercion, and thus experience fewer instances of aggression (Watson-Capps 2005). Consequently, we predict that young adult females (10–13 years, typical age of first conceptions) would have higher tooth rake prevalence than experienced females (> 13 years) who have probably been consorted with during at least one or more breeding seasons. We also hypothesized that there would be a sex effect on conflict rate. In addition to receiving aggression via sexual coercion, juveniles commonly participate in mixed-sex social groups (Krzyszczuk et al. 2017) and may consequently acquire more tooth rakes. However, since females are rarely aggressive and avoid males (Scott et al. 2005; Galezo et al. 2018), we predict females would receive fewer attacks than their more aggressive male counterparts. We also predict that juvenile females would have more tooth rake scars than adult females from their encounters with juvenile males. Although adult females receive significantly more tooth rake scars when cycling than other reproductive states (Scott et al. 2005), cycling periods are relatively infrequent given the long lactation period (Mann et al. 2000; Karniski et al. 2018).

Methods

Study population and site

The data for this study come from the longitudinal Shark Bay Dolphin Research Project (SBD RP) whereby approximately 1700 individually recognized wild Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia (25° 47' S, 113° 43' E) have been studied for over 30 years. Dorsal fins and body pigment are used to differentiate between individual dolphins (Bichell et al. 2018). The sex of a dolphin is determined by opportunistic views of the genital area and/or the presence of a dependent calf (Smolker et al. 1992), and in some cases, DNA (Krützen et al. 2004). The age of a dolphin is determined by known or estimated birthdates, which are established based on sightings as a calf, physical and behavioral characteristics (Mann and Smuts 1999), and/or through ventral speckling (Krzyszczuk and Mann 2012). Calves are defined as still nursing; the average weaning age is 4 years (Mann et al. 2000; Karniski et al. 2018). The juvenile period is defined post-weaning to age 10, the earliest age at first birth (Karniski et al. 2018). The average age of first birth is 13 years (Mann 2019). Therefore, the following age classes were used:

calves are considered to be 0 to 4 years, juveniles 4 to 10 years, and adults > 10 years (Karniski et al. 2018).

Survey and follow records

Data collected by the SBD RP primarily consist of observational, boat-based surveys, and focal follows (Karniski et al. 2014). Both methods provide opportunities for photographs and observational notes on behavior and physical attributes. For this study, we included photographic and scarring data collected during surveys and focal follows from 1988 to 2016. It was not possible to record data blind because our study involved focal animals in the field.

Tooth rake assessment

Tooth rakes, superficial wounds received from other dolphins and a sign of conspecific aggression, are identified by close parallel lines of depigmentation and/or broken skin (Fig. 1).

Although sharks are another major source of scars, the markings acquired from sharks differ from the aforementioned conspecific acts of aggressions in several ways. Compared to shark rakes, conspecific rakes tend to be smaller, shallower, and have fewer lines associated with them. Shark bites tend to have a more circular pattern with deeper and far more teeth marks (Heithaus 2001). Overall, the patterns associated with conspecific scars are distinct from those acquired from heterospecific interactions. Body sections that are viewed or photographed can be classified on the state of the tooth rake (Fig. 2). A new tooth rake (Fig. 2a) is characterized by broken skin, a deep black wound, hanging flesh, and/or blood. An obvious tooth rake (Fig. 2b) is characterized by no breaks in the skin, depigmentation, and/or the colors white/gray. Faint tooth rakes (Fig. 2c) exhibit no breaks in the skin, faded depigmentation, and/or the colors white/gray. Tooth rake

absence (Fig. 2d) is coded when there were no signs of tooth rakes based on photographs. During field observations, the presence of scars is often noted, but the tooth rake absence is rarely mentioned. Due to this bias, tooth rake absence was retrospectively coded based on photographs.

Photographs

During the process of data collection, photographs of individual and/or groups of dolphins were taken at instances when the dolphins come to the water surface to breathe. The photographs were then cataloged and uploaded to the database for future reference and use. Currently, there are over 70,000 photograph records in the database, but only 199 photographs were used to determine healing time because we focused on photographs of individuals that definitively showed new tooth rakes, followed by photographs within and across years that showed their fading and eventual absence.

Healing time

To determine the average healing time for tooth rakes, we restricted analysis to dolphins that had new rakes where at least one subsequent stage (obvious or absent) was recorded. We calculated the number of days between the photograph of a new rake and each subsequent stage. No maximum cutoff for the number of days between the initial and last sighting of a tooth rake was used (min = 87 days, max = 2240 days). The progression of a new tooth rake was followed until (1) there were no additional photographs or (2) a photograph indicated an absence of the tooth rake. Tooth rakes without a subsequent photograph proving their eventual absence were excluded from the sample. We did not use photographs where we could not be sure of tooth rake presence or absence because of lighting (backlit or low-light), distance to subject, and poor focus

Fig. 1 New tooth rakes indicated by the clusters of black parallel streaks on the left lateral side and dorsal fin of a wild bottlenose dolphin (square). The semi-circular scar posterior to the dorsal fin is a shark bite scar (arrow). Shark bite scars such as these tend to be permanent

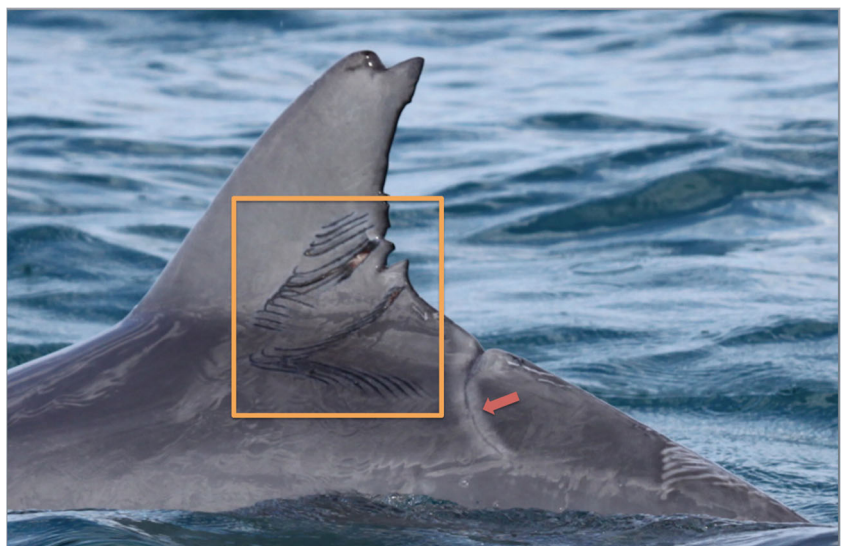
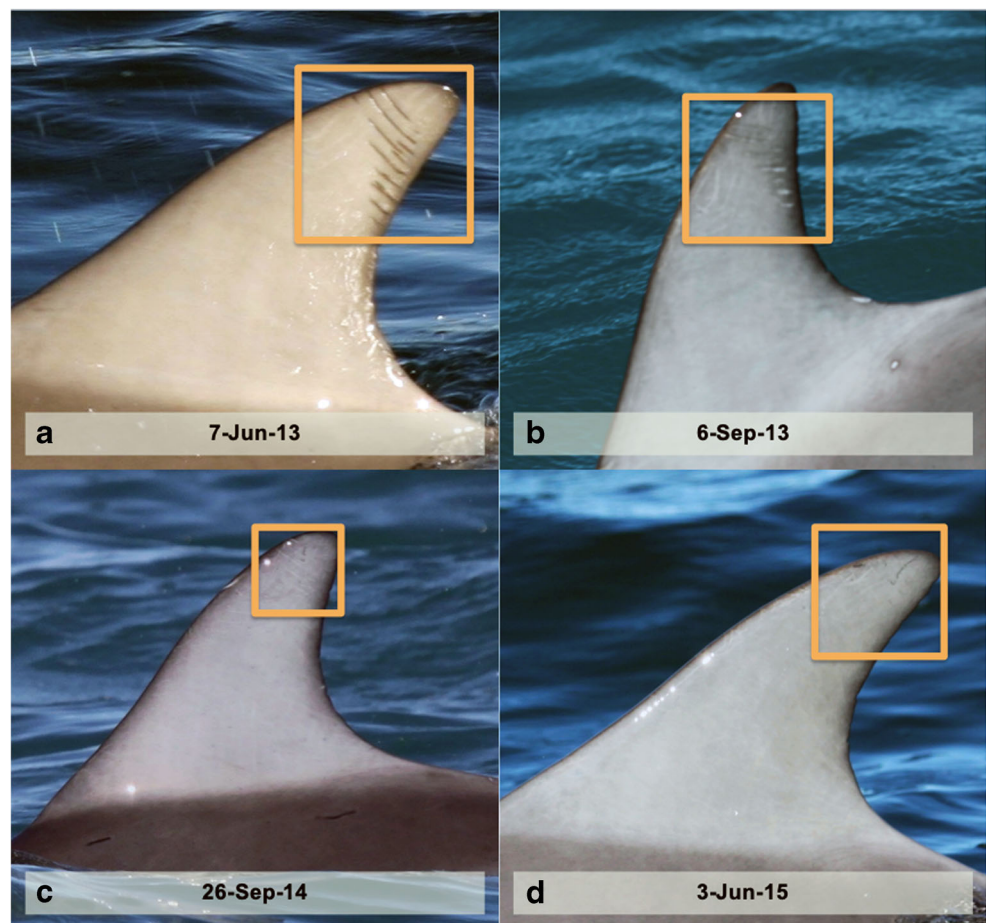


Fig. 2 The healing progression of a tooth rake scar in a single individual over time. The four classifications of wound state are new (a), obvious (b), faint (c), and absent (d)



that could obscure tooth rake scars. Only photographs in which the tooth rake or the location of the healed tooth rake was clearly visible were used (number of different tooth rakes = 70; number of different dolphins = 52: 26 females, 26 males). Once all the photographs of new tooth rakes and subsequent absent tooth rake sightings were identified, an average number of days were calculated and converted into years for a preliminary healing time.

To determine how long tooth rakes are visible, we conducted a right interval-censored survival analysis using the *icenReg* package in R version 3.4.0 (R Core Team 2017). This method uses a non-parametric maximum likelihood estimator in cases where the interval is not closed, generating two curves in between which lie the maximum likelihood estimation (Anderson-Bergman 2017). Data for each tooth rake generally consisted of two values: (1) the number of days between an initial photograph of a new tooth rake and the last photograph of the same tooth rake when it was still visible (obvious or faint) and (2) the number of days between an initial photograph of a new tooth rake and a subsequent photograph of the tooth rake fully healed and no longer visible (absent). These two values per tooth rake served as the interval range for the analysis. In cases where there were no photographs indicating

the eventual absence of a tooth rake or when only one subsequent photograph of the tooth rake was available, only the number of days between the initial photograph and the last available photograph (obvious, faint, or absent) was used and censored. The healing time was determined by locating the point on the survival curve at which the majority of tooth rakes (> 90%) were no longer visible. The same survival analysis was used to compare the sexes.

Demographic profiling

Physical and demographic data from the long-term database, acquired from both photographs and surveys, were compiled every year for every individual that acquired a new tooth rake. The individual was scored as having a tooth rake (1) regardless of the number (≥ 1) of new tooth rakes the individual acquired in that year, or left blank if there was no evidence for tooth rakes. Absences could not be scored because of the aforementioned bias against reporting an absence and because the individual could have tooth rakes on areas of the body that were not photographed. This resulted in a sample size of 269 different tooth rakes.

To determine the baseline demographic distribution, we calculated the number of individual dolphins (for each age and sex) for each year from 1999 to 2016 from available sighting data. The subsequent values were then used to calculate the average values corresponding to each age and sex combination over the entire time period. The year 1999 was selected as a cutoff because prior to 1999, the data on new tooth rakes were sparse, largely due to the shift from 35-mm film to digital photography, which facilitated post hoc coding. The age- and sex-specific tooth rake prevalence data were then converted into proportions by dividing the number of individuals with new tooth rake scars for each age-year by the yearly average number of individuals in the population. Age 30 was used as the cutoff because age assignments are less accurate for individuals born well before 1984, the onset of the SBDRP. The resulting proportions were then visually investigated using a Loess smoothing curve.

A logistic regression model was used to examine the effects of sex and age on the prevalence of new tooth rakes. Model coefficients were bootstrap resampled 10,000 times (with replacement). Each time, the model randomly extracted a data point (i.e., a single tooth rake) for each individual and compiled a new set of tooth rake prevalence data to run through the model in order to ensure a unique set of IDs. Fixed factors were age (rounded down to the year) at tooth rake acquisition and sex. Based on a visual examination, we used a quadratic regression to analyze tooth rake prevalence from ages 13 and under ($N=60$ males, 55 females), and a linear regression to analyze tooth rake prevalence from ages 13 and up ($N=69$ males, 25 females). Age 13 was used as the dividing age as most individuals are presumed sexually mature (fertile) by then, and the Loess smoothing curve exhibited a parabolic trend below age 13 and a linear trend above age 13.

Results

Healing

The average healing time of tooth rakes in Indo-Pacific bottlenose dolphins was 584.2 days or 1.6 years. Using the right interval-censored survival analysis, we found that 90% of males and 95% of females healed within a year (Fig. 3). The sex difference in healing times (new to absent) was significant ($N=70$, $P<0.001$), in that males healed slower than females.

Age and sex

The Loess smoothing curve (Fig. 4) shows high tooth rake prevalence for both sexes during the juvenile period. Surprisingly, both males and females exhibited a decline in tooth rake prevalence around age 10, just when they were approaching sexual maturity. Tooth rake prevalence increased

again among both sexes from age 13 to 30. Males generally displayed greater tooth rake prevalence than females. The quadratic regression revealed age ($t=-10.409$, $P<0.001$, $N=115$) and sex ($t=2.679$, $P<0.001$, $N=115$) effects on tooth rake prevalence for dolphins ages 0 to 13, with an initial increase during the calf period before decreasing near sexual maturity. The linear regression revealed age ($t=7.354$, $P<0.001$, $N=94$) and sex-effects ($t=6.879$, $P<0.001$, $N=94$) on tooth rake prevalence from 13 to 30, with prevalence increasing consistently with age, and again males having more rakes than females.

Discussion

Although a few studies have examined wound healing and sex differences in aggression among cetaceans, this is the first to explore how the patterns of healing and aggression change depending on sex and age across the lifespan. We found a sex effect on tooth rake healing time, in that female dolphins healed faster than their male counterparts. There may be two reasons for this difference in healing time: (1) sex differences in immune response and (2) sex differences in aggression severity. Human females heal faster from dermal wounds than males (Ashcroft et al. 1997; Jorgensen et al. 2002; Ashcroft and Ashworth 2003), attributable to their higher levels of estrogen compared to males, which in turn affect cellular processes (Ashcroft et al. 1997; Ashcroft and Ashworth 2003). This may be the case in Indo-Pacific bottlenose dolphins. Second, as male Indo-Pacific bottlenose dolphins are more aggressive than the females (Scott et al. 2005), conflict is more likely to escalate between males, which might result in deeper and more serious injuries in males than females. These explanations are not mutually exclusive and either could explain the slower healing time among male relative to female dolphins. The plateauing of tooth rake presence above 0 (Fig. 3) suggests that tooth rakes still present after roughly 400 days are likely permanent or, in the case of a few of our data points, outliers that remain faint for much longer.

Our results on tooth rake prevalence and its demographic distribution are consistent with the hypothesis that there would be age and sex effects on the prevalence of new tooth rakes, with some surprising findings. Juvenile dolphins of both sexes had more new wounds than older dolphins (Fig. 4). High tooth rake prevalence among juvenile males may be the product of competition before stable networks have been formed (Scott et al. 2005). The juvenile period is clearly one of vulnerability, as males must establish partners to protect themselves from attacks by older males (Stanton and Mann 2012). High tooth rake prevalence among juvenile females may be the result of frequent interactions with juvenile male dolphins (Krzyszczuk et al. 2017). Additionally, it is important to note that tooth rakes are superficial wounds and do

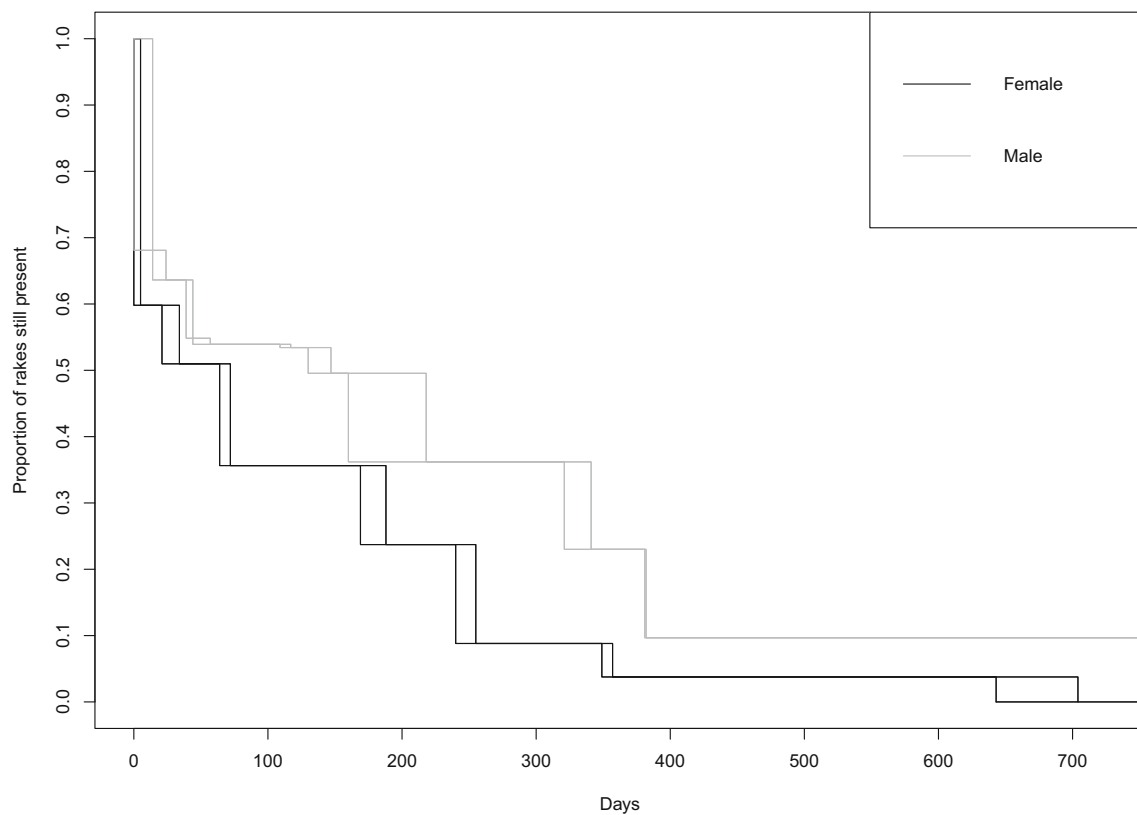
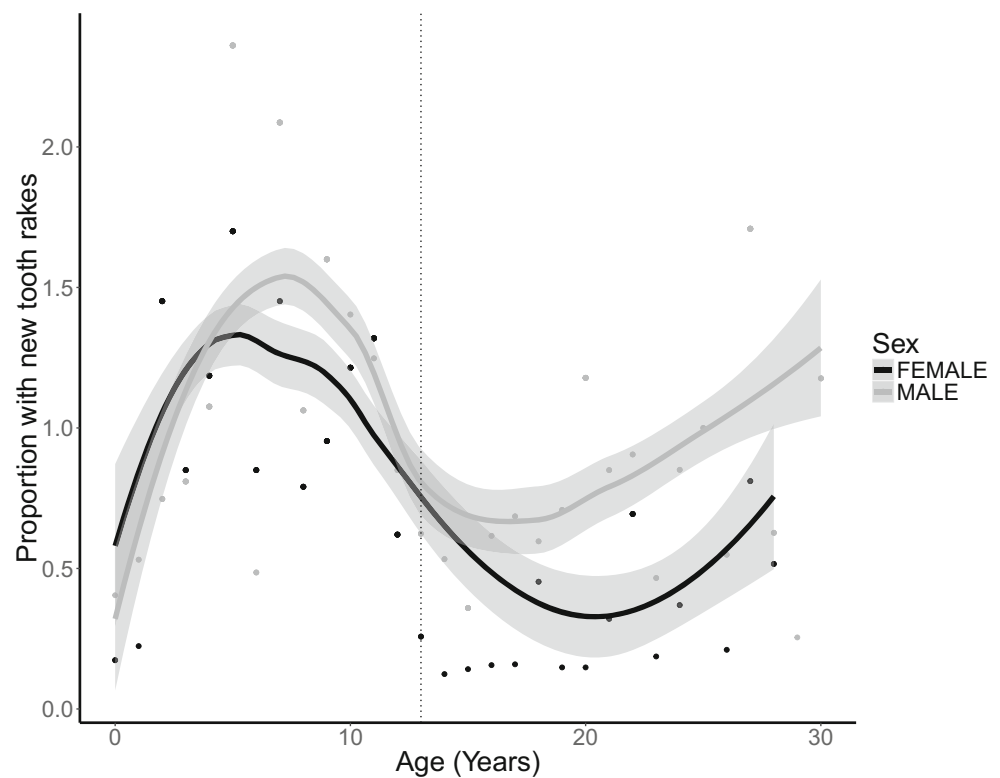


Fig. 3 The relationship between sex and the number of days before a new tooth rake was no longer visible. Ninety percent of tooth rake scars in males and roughly 95% in females fully heal within 400 days. The sex difference in healing times was significant ($P < 0.001$)

Fig. 4 Loess smoothing curve of new tooth rake prevalence in relation to age and sex. Dots indicate the proportion of individuals that had new tooth rakes within each age-year class, separated by sex. The light gray area indicates 95% confidence intervals. A quadratic regression revealed age and sex effects on tooth rake prevalence for dolphins from birth to 13 years. A linear regression revealed age and sex effects on tooth rake prevalence for dolphins from age 13 to 30. The dotted vertical line indicates age 13



not represent serious aggressive behaviors such as ramming, body slams, and tail hits, which might be more lethal (e.g., Parsons et al. 2003; Lusseau 2006).

Tooth rake prevalence started to decline around age 10, and noticeably declined by about age 13, for both sexes. These declines are interesting to note, as this is roughly the age range in which dolphins reach sexual maturity and are categorized as adults (Cheal and Gales 1992; Kemper et al. 2014). This pattern is more difficult to explain without more detailed behavioral observation. Either males have formed stable bonds that might buffer them from attacks, or, as they reach adulthood and are in direct competition with larger and older adult males, they might withdraw from or avoid social encounters. In early adulthood, males may not engage in as many instances of competitive play and sexual practice behaviors as they did during the juvenile period (Scott et al. 2005; Mann 2006). We suspect that most tooth rakes received during the juvenile period are a result of sociosexual play, which involves extensive physical contact. However, the sharp decrease in early adulthood was not expected and shows the importance of more detailed, long-term, and longitudinal conflict data. Previous studies demonstrating high conflict in adult males did not differentiate between young and older adults (Connor et al. 1996; Scott et al. 2005). Although some of the young adult males have strong bonds with each other, their alliances may be unstable and unreliable, and this could enhance their vulnerability. We suggest that during the sub-adult period, when males are transitioning from juvenile to adult, they might withdraw from social encounters to avoid eliciting aggression from older males with whom they are now in direct reproductive competition. It should be noted that as sub-adults, male dolphins are fertile and nearing full body size, but are not socially mature (i.e., in alliances). This would explain why tooth rake prevalence among males increases again when the dolphins are in their mid-teens, when male alliances are thought to stabilize. Similarly, several primate studies (e.g., *Colobus vellerosus*, *Cebus capucinus*, *Hylobates lar*) have found that sub-adult males exhibit lower aggression rates than older adult males (Bartlett 2003; Fedigan and Jack 2004; Teichroeb et al. 2014).

The decrease in tooth rake prevalence in females upon reaching adulthood could relate to several different factors. First, upon reaching sexual maturity, females likely reduce their interactions with male juveniles (Wallen et al. 2017) and thereby receive fewer injuries from juvenile males. In this regard, there may be a gap between onset of sexual maturity and first reproduction, during which females are likely to receive attacks from adult males. Since we defined adulthood from the age of 10, but only a few females reproduce before age 12, young females might not be targeted as often. Since younger females have higher reproductive value than older females (Karniski et al. 2018) these results remain puzzling and require more detailed investigation. Specifically, a close examination of age-specific

tooth rake prevalence in relation to reproductive state, with repeated measures of females through time, would help determine what factors increase female vulnerability to male attacks.

Although the use of tooth rakes as a proxy for conflict rates in dolphins at different life history stages is promising, it should be noted that the use of tooth rake prevalence will most likely result in an underestimate of conflict rate. Individual dolphins may engage in frequent contest behavior and not have any rakes to show for it. It is also possible that, given the factors of chance encounters and the limited amount of a dolphin's body surface visible at any given time, tooth rakes were missed and went unobserved. However, we argue that patterns of tooth rake prevalence have captured age and sex-specific patterns of conflict.

To date, no study on cetaceans has documented a sex difference in healing time or investigated age-specific changes to patterns of conspecific aggression. Currently, there are only a few cetacean studies on healing and the demographic differences in conspecific aggression, and most of them are fairly general in their findings. Lockyer and Morris (1990) have found that tooth rakes disappear after 5 to 20 months. Scott et al. (2005) explored tooth rake prevalence in different demographic groups, but their findings are framed within the more general age-class categories (i.e., calves, juveniles, and adults). Our study contributes to the study of healing and social conflict in cetaceans in several ways. First, we established precise healing times in dolphins and demonstrate that males heal more slowly than females. Second, we used detailed life history data and a large sample size to determine patterns of conspecific aggression across the lifespan. These patterns reveal results that raise new questions about the importance of social interactions, bonds during the juvenile period, and the transition to adulthood.

Our study has shown two primary results. First, tooth rake healing is slower for males than females, possibly due to the severity of wounds or physiological sex differences. Secondly, both sexes have high wounding rates in the juvenile period, with a decrease in wounding rate around age 10 (sexual maturity) and an increase during late adulthood. The age variation in tooth rake prevalence may be attributed to a variety of life history events of wild Indo-Pacific bottlenose dolphins. Future work should focus on the direct connection between wounding and life history patterns. More specifically, it would be worthwhile to examine this relationship in older adults. In addition, the individual differences in wounding rate and their correlation with the individual's reproductive state and social position in the broader network might also be explored.

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Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This work was approved by the Georgetown University Animal Care and Use Committee (permits 07-041, 10-023, 13-069), DBCA (permits SF009311, SF008076, SF009876), and The University of Western Australia (animal ethics permit 600-37). All procedures performed in this study were in accordance with the ethical standards of the aforementioned institutions and agencies.

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